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Effects of abscisic acid and gibberellin on sugar accumulation in 'Fengtang' Plum (*Prunus salicina* Lindl.)

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Abstract: To investigate the regulation mechanism of exogenous plant growth regulators on the sugar accumulation of 'Fengtang' plum fruits, and to provide theoretical support for improving the sugar content of 'Fengtang' plum fruits. The expression of fruit sugar fractions and related genes was determined by spraying different concentrations of exogenous abscisic acid (ABA) and Gibberellic acid 3 (GA_3) during the critical period of sugar accumulation in 'Fengtang' plum. The results showed that exogenous ABA treatment increased fruit soluble solids content, delayed the decline in fruit firmness, increased fruit sucrose and sorbitol content and decreased glucose and fructose content at 90 and 100 days after flowering, while exogenous GA_3 treatment decreased fruit sorbitol and sucrose content and increased glucose and fructose content at 110 days after flowering; Exogenous ABA treatment significantly increased the expression of the fruit sugar transporter protein genes *PsSWEET4* and *PsSTP1* as well as the sucrose phosphate synthase genes *PsSUS4* and *PsSPS2* at 90 and 100 days after flowering, whereas exogenous GA_3 treatment increased the expression of the neutral converting enzyme genes *PsNINV1/3/4* at 90, 100, and 110 days after flowering to convert sucrose to fructose and glucose. The conclusion is that ABA increases fruit sugar content by increasing the expression of the fruit sugar transporter protein genes *PsSWEET4* and *PsSTP1* as well as the sucrose synthase genes *PsSUS4* and *PsSPS2*, whereas GA_3 decreases sugar accumulation and delays fruit ripening by decreasing the accumulation of sugar during ripening by increasing the expression of the neutral transforming enzyme genes *PsNINV1/3/4* to break down sucrose into fructose and glucose.

Keywords: 'Fengtang' plum; exogenous plant growth regulator; soluble sugar; abscisic acid; gibberellic acid

'Fengtang' plum is a characteristic geographical indication plum (*Prunus*) species found in Guizhou Province, China, in recent years, which was propagated from local wild resources by superior grafting of scions (Zhang et al. 2018), and its fruits are rich in a variety of soluble sugars and dietary fibres and other nutrients (Huang et al. 2022; Zhang et al. 2023), while the organic acid content was only 5.94 mg/g FW at maturity (Wang et al. 2018), which belongs to the typical high-sugar and low-acid-accumulating plum varieties (Børve et al. 2023).

Soluble sugar content determines fruit sweetness and thus affects taste (Cirilli et al. 2016), and in drupe fruits, soluble sugar fractions are mainly sucrose, fructose, glucose, and sorbitol (Baldicchi et al. 2015; Desnoues et al. 2018), whereas in plum, soluble sugars are mainly dominated by glucose, fructose and sucrose (Jiang et al. 2023). 'Fengtang' plum mature fruit sucrose content reached 36.29 mg/g FW and soluble sugar content reached 80 mg/g FW (Nie et al. 2023), while in 'Xiang' plum mature fruit sucrose content was only 28.15 mg/g FW and the or-

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ganic acid content reached 15.76 mg/g FW (Lin et al. 2023). Glucose and fructose predominate in the early stages of peach, plum, and apricot fruit development, and glucose and fructose are synthesized into sucrose in the cytoplasm by transporter proteins and sucrose synthase during ripening (Gao et al. 2003; Bae et al. 2014). Whereas phytohormones play an important role in sugar synthesis and catabolism metabolic pathways and determine soluble sugar content, it has been found that spraying abscisic acid (ABA) can increase soluble sugar content in navel orange and grape fruits (Rehman et al. 2018; Li et al. 2020; Li et al. 2021), and that gibberellin acid (GA) has the effect of increasing fruit hardness and delaying fruit ripening (Cline, Trought 2007), and also increases the weight of plum (Muharram et al. 2021) and apple (Liu et al. 2022), and increases the storage tolerance of post-production fruits. In-depth studies have revealed that GA_3 delays fruit ripening mainly by inhibiting carotenoid synthesis, outward transport of ethylene precursors, and conversion of fructose and glucose (Wu et al. 2023), and also interacts with cytokinin (Suwandi et al. 2016).

Currently, studies on sugar accumulation in 'Fengtang' plum mainly focus on physiological and transcriptional levels (Nie et al. 2023; Wang et al. 2023), and there is a lack of studies on external regulatory factors for its high sugar accumulation. Based on this, we sprayed different concentrations of exogenous ABA and Gibberellic acid 3 (GA_3) during the critical period of sugar accumulation in 'Fengtang' plum (80, 90 and 100 days after flowering), and measured the contents of major sugar components and the expression of key genes in the fruits by High Performance Liquid Chromatography (HPLC), to investigate the regulatory effects of exogenous ABA and GA_3 on the accumulation of sugar in the fruits, in order to provide a better solution for the regulation of sugar accumulation in the fruits. We investigated the role of exogenous ABA and GA_3 in the regulation of fruit sugar accumulation, and provided new technology and theoretical support for the sugar accumulation and quality improvement of 'Fengtang' plum.

MATERIAL AND METHODS

Materials and Reagents

Plant materials. The material was taken from the base of 'Fengtang' plum in Broken Fir Town, Huishui County, Qiannan Prefecture, Guizhou Province (106°33'19"E, 25°50'45"N) at an altitude of 1 081 m a.s.l. The orchard has a sandy soil, pH = 5.5 ~ 6.5, and the tree is 7 years old with an open-heart type.

Test reagents. ABA (analytically pure (AR), Aladdin, USA), GA_3 (analytically pure, Aladdin, uas), Tween 80 (chemically pure, Kemiou, P. R. China), glucose, fructose, sucrose, sorbitol (AR analytically pure, Chengdu Jinshan, P. R. China), acetonitrile (chromatographic grade, Aladdin), polysaccharide polyphenol plant RNA extraction kit (Tiangen, Beijing), reverse transcription and qRT-PCR kit (TaKaRa, Beijing).

Instruments and equipment. GY- hardness tester (Zhejiang Toppan Yunnong Science and Technology Company), WZ-108 Digital Saccharometer (ATAGO, Japan), CP213 Electronic Balance (Haus, USA), 2-JR Freezing Centrifuge (TOMOS, USA), Pipette Gun (Eppendorf, Germany), K5500 Ultramicro Spectrophotometer (Thermo Fisher Scientific, USA), High Performance Liquid Chromatograph (Thermo Fisher Scientific, USA), ABI ViiA7DX Fluorescence Quantitative PCR System (Thermo Fisher Scientific, USA).

Test treatment. The experiment was conducted from May 30, 2022 (80 days after flowering) to June 20, 2022 (100 days after flowering) by spraying exogenous ABA and GA_3 on the fruits until droplets fell from the fruits for three times, and the samples were taken at an interval of 10 days after each spray. The chemicals were mixed with 0.1% Tween 80 to increase the absorption of the chemicals. The treatments were 25 mg/L ABA (ABA-25), 50 mg/L ABA (ABA-50), 75 mg/L ABA (ABA-75), 25 mg/L GA_3 (GA-25), 50 mg/L GA_3 (GA-50), 100 mg/L GA_3 (GA-100), and Control. Three biological replicates for each treatment, seven treatments totalling 63 fruit trees, each sampling each tree from the four sides of the orientation of five fruits, each treatment of each period of time to select the size of 180 fruits of uniform uniformity as a sample chopped liquid nitrogen flash-freezing, put –80 °C preservation of standby.

Determination of single fruit weight, hardness and soluble solids. An electronic balance was used to determine the single fruit weight. After peeling 1 mm of the fruit, a GY-4 type fruit hardness tester was used to take points on both sides of the suture line in a symmetrical position to apply the same force to determine the hardness of the fruit flesh. Fruit flesh soluble solids were determined by WZ-108 digital saccharimeter.

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Determination of fruit sugar fraction content. The determination of soluble sugar fractions and contents in the fruit was improved by referring to the method of Wang et al. (2018). 1.00 g of fruit pulp was weighed and ground into homogenate with 5 mL of ultrapure water, and the supernatant was ultrasonically separated and filtered through microporous filter membrane for use. Sucrose (0.40 g), glucose, fructose and sorbitol (0.50 g) were accurately weighed and dissolved in ultrapure water to 10 mL, and then prepared into mixed standard solutions with different concentration gradients, and then filtered through 0.22 μm microporous filters and placed in 1.5 mL injection bottles. The components and contents of fructose were determined by HPLC with the mobile phase of mixed acetonitrile/water (75/25,V/V), the column temperature at 30 °C, the detector cell temperature at 35 °C, the flow rate of 1.0 mL/min, and the injection volume of 10 μL.

RNA extraction and concentration measurement. All required plastic consumables were sterilized at 121 °C for 20 minutes and dried in a special oven. Weigh 0.5 g of the sample into a frozen centrifuge tube, and use the RNA extraction kit to extract total RNA in strict accordance with the instructions of the kit. The total RNA extracted was used to determine the concentration and purity of the RNA by nucleic acid proteomics instrument, and 1 μL of the total RNA was aspirated for the integrity test after preparation of 1% Gelred staining of the agarose gel.

cDNA synthesis. The synthesis was performed according to the TaKaRa Reverse Transcription Kit, and the synthesis was completed in two steps, the first step: remove the DNA in the genome, the reaction conditions were 42 °C, 2 minutes, or room temperature static for 5 minutes, and stored at 4 °C. Step 2: reverse transcription reaction was performed to reverse transcribe RNA to cDNA, the total system was 20 uL: the reaction conditions were: 37 °C, 15 min; 85 °C, 5 s. Store at 4 °C.

Primers design and synthesis. According to the principle of fluorescent primer design, the primers for fluorescence quantification of each gene in this experiment were designed using Primer-Blast from NCBI online website, and then handed over to China Sangong Bioengineering Company Limited (Shanghai, China) for synthesis. The specific primer sequences are shown in Table 1.

qRT-PCR amplification. The subunit family proteins (CAC) in the lattice protein articulator complex were used as the internal reference genes (You et al. 2016), and PCR reactions were performed using an ABI ViiA7DX fluorescence quantitative PCR instrument. Fruit cDNA from each developmental stage of different treatments were used as templates for mixed amplification using SYBR Premix Ex Taq premixed enzyme solution from TaKaRa. The mixing system was 20 μL: 10 μL of TB Green premix system (2X); 0.8 μL of upstream primer (10 μmol/L); 0.8 μL of downstream primer (10 μmol/L); 2 μL of template; 6.4 μL of ddH_2O. The data were analysed by the $2^{-\Delta\Delta CT}$ method at the end of the reaction.

Statistical analysis and graphics. Data were statistically analysed using IBM SPSS Statistics 26 and plotted using Origin 2021. Data were analysed using *t*-test with one-way analysis of variance (ANOVA) at a significant level of $P \leq 0.05$. Values are expressed as mean ± standard error.

RESULTS

Regulation of fruit quality by exogenous ABA and GA_3. 'Fengtang' plum fruit development was fully matured at 110 days after flowering, while the large accumulation of soluble solids started at 80 days after flowering, and exogenous ABA and GA_3 significantly regulated fruit weight per fruit, soluble solids and hardness (Table 2). After hormonal treatment of 'Fengtang' plum fruits at 80 days after flowering, it was found that the single fruit weight of different treatments increased linearly with fruit development, with control fruits increasing from 40 g at 90 days after flowering to 65 g at 110 days; The 25 mg/L ABA treatment significantly increased single fruit weight from 45.69 g initially to 72.37 g at 90–110 days after flowering, whereas GA_3 spraying significantly inhibited the increase in single fruit weight at 90–110 days after flowering and the negative regulation appeared to be intensified with the increase in concentration. At 110 days after flowering, 25 mg/L ABA had the best effect on the increase in single fruit weight with 6.8%.

ABA treatments effectively retarded the decline in fruit firmness, which was significantly retarded by spraying 50 mg/L and 75 mg/L at 90–110 days. The 75 mg/L ABA treatment significantly increased the firmness of control fruit by 11.7% at 110 days after flowering (Table 2); GA_3 treatments did not significantly regulate fruit firmness at 90 days after flowering, whereas 25 mg/L GA_3 significantly reduced fruit firmness at 100 days, and all treatments

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Table 1. qRT-PCR primers for 12 key genes for sugar accumulation

Gene ID	Gene names	Primers (5'–3')
gene.evm.model.LG07.772	*PsSUS4*	F: CGAACTCGTTGCCCTTCTCT R: CGAACTCGTTGCCCTTCTCT
gene.evm.model.LG01.2621	*PsSPS2*	F: CTGTTGAACGTGACACTGGA R: GGACTTCCCCGTAAGACACC
Prunus_salicina_newGene_262	*PsNINV3*	F: GCATAGCAGATCAGGAGGCA R: CGGCTGGGGAGACAACTTAC
gene.evm.model.Contig2.37	*PsNINV4*	F: ATTCCGTGACCCAACAACGG R: CGAGTGAAGTGGGTGATGGG
gene.evm.model.LG06.1462	*PsNINV1*	F: CACCACAGATCAGGAGGCAA R: TCCCATCCTGCAGAAGGAAC
gene.evm.model.LG01.1561	*PsHXK1*	F: GACGCATTCAAGGATGGGGA R: CGGAAACTTCCTCTCCAAGCA
gene.evm.model.LG04.2538	*PsHXK3*	F:TGTGATGTTGTGACCCGTAGG R: ACTCCCATCCCGACCAATCT
gene.evm.model.LG01.1216	*PsPGM1*	F: GCAGTGTTCCCCTGCTTTTG R: ACCATCCATCCTTGCCAGTC
gene.evm.model.LG02.786	*PsUGP1*	F:CTCTGGTCTCCGCAAGAAGG R: CTTTATCCGCTGGAAGGGCA
gene.evm.model.LG03.1388	*PsUGP2*	F: GGAAGGGTGCAACTGTACGA R: GGAGGCAAACCCCAGTTTCT
gene.evm.model.LG01.8053	*PsSTP1*	F: TGGCGACTTTACCGACATCC R: ACGAACACTCTCTGCTGTGG
gene.evm.model.LG08.506	*PsSWEET4*	F: GCACATGGTATGGATCGCCT R: AACTGAAACACTGCACCAGC
At1g60780	*CAC(Actin)*	F: GGGATACGCTACAAGAAGAATGAG R: CTTACACTCTGGCATACCACTCAA

of GA_3 sprays significantly reduced fruit firmness at 110 days. Interestingly, the lower the concentration of GA_3, the lower the firmness.

It was found that ABA treatment significantly increased the fruit soluble solids content (Table 2). At 90–100 days after flowering 50–75 mg/L ABA was found to act as an increase in soluble solids and then 110 days at 25–75 mg/L ABA all significantly increased the soluble solids content and 50 mg/L was found to be the most effective as it significantly increased the soluble solids content by 26.97% in comparison to the control. GA_3 treatment did not significantly affect fruit soluble solids, while 50 mg/L significantly reduced soluble solids content at 110 days instead.

Regulation of fruit sugar fractions by exogenous ABA and GA_3. As can be seen in Figure 1, the trends of sorbitol and sucrose contents were consistent, and glucose and fructose contents were relatively consistent. It was found that sorbitol and sucrose content appeared to increase to varying degrees as the fruit ripened (Figure 1A and 1D). ABA treatment for 90 days significantly increased the sorbitol content and the sorbitol content of different concentrations of ABA was at 6 mg/g FW, and the effect disappeared as fruit development matured and the number of sprays increased; ABA treatment significantly promoted sucrose accumulation at 90 days after anthesis, which increased by 47.50% compared to CK, and finally the sucrose content of ABA-treated fruits increased from 13.28 mg/g FW at 90 days after anthesis to 38.16 mg/g FW at 110 days after flowering. GA_3 treatment significantly reduced sorbitol content and the reduction was more pronounced with fruit development and the number of sprays, with the content increasing only from 3.1 mg/g FW at 90 days after flowering to 7.1 mg/g FW at 110 days. The effect of the GA_3 treatment on sorbitol content was more

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Table 2. Effect of exogenous ABA and GA_3 on fruit quality of 'Fengtang' plum

Treatment	Fruit weight (g)	Fruit firmness (kg/cm^2)	Total soluble solids (°Brix)
90 days after flowering			
ABA-25	45.69 ± 2.85^{a}	16.28 ± 0.76^{ab}	6.89 ± 0.51^{b}
ABA-50	43.57 ± 4.61^{b}	16.6 ± 1.02^{a}	7.56 ± 0.71^{a}
ABA-75	41.27 ± 7.03^{c}	17.04 ± 0.78^{a}	7.24 ± 0.54^{ab}
GA-25	38.75 ± 2.66c^{d}	14.28 ± 1.34^{b}	6.25 ± 0.34^{b}
GA-50	35.27 ± 2.96^{d}	14.6 ± 1.46^{b}	6.02 ± 0.55^{b}
GA-100	35.62 ± 3.07^{d}	14.04 ± 1.49^{b}	6.01 ± 0.41^{b}
Control	40.33 ± 3.23^{c}	15.27 ± 1.09^{b}	6.46 ± 0.41^{b}
100 days after flowering			
ABA-25	55.66 ± 2.57^{a}	12.36 ± 1.61^{ab}	12.86 ± 0.87^{ab}
ABA-50	53.62 ± 2.38^{ab}	12.49 ± 0.92^{ab}	13.59 ± 0.84^{a}
ABA-75	54.27 ± 2.9^{a}	12.95 ± 1.16^{a}	13.75 ± 0.65^{a}
GA-25	45.36 ± 2.28^{c}	11.04 ± 0.95^{c}	11.88 ± 0.72^{b}
GA-50	44.27 ± 5.35^{c}	11.69 ± 1.66^{b}	11.51 ± 0.73^{b}
GA-100	44.04 ± 5.18^{c}	11.75 ± 2.95^{b}	11.37 ± 0.38^{b}
Control	51.33 ± 4.59^{b}	12.01 ± 0.62^{b}	11.02 ± 0.74^{b}
110 days after flowering			
ABA-25	72.37 ± 4.61^{a}	10.88 ± 1.41^{a}	13.53 ± 0.86^{c}
ABA-50	69.11 ± 7.03^{ab}	11.20 ± 1.07^{a}	16.10 ± 1.51^{a}
ABA-75	65.18 ± 8.44^{c}	11.29 ± 0.76^{a}	15.03 ± 1.48^{b}
GA-25	65.88 ± 9.05^{c}	7.63 ± 1.02^{d}	12.43 ± 1.20^{d}
GA-50	67.75 ± 4.81^{b}	8.96 ± 0.78^{c}	11.35 ± 0.60^{e}
GA-100	59.73 ± 6.47^{d}	9.09 ± 0.74^{c}	12.57 ± 0.60^{d}
Control	67.74 ± 7.03^{b}	10.11 ± 1.07^{b}	12.68 ± 1.01^{d}

*ABA-25, 50, 75 represents the concentration of exogenous ABA sprayed at 25 mg/L, 50 mg/L, and 75 mg/L. GA-25, 50, 100 represents the concentration of exogenous GA_3 sprayed at 25 mg/L, 50 mg/L, and 100 mg/L. control denotes clean water spraying; $^{a-c}$indicate significant differences ($P \leq 0.05$) according to the Duncan test

pronounced with fruit development and the number of sprays; In contrast, GA_3 treatment sucrose content was significantly lower than CK from 90–110 days after flowering, and sucrose content only increased from 7.69 mg/g FW to 26.25 mg/g FW.

Changes in fructose and glucose content showed an opposite trend compared to sorbitol and sucrose, with an overall decrease in content as the fruit developed and matured (Figure 1B and 1C). Fructose and glucose sugar content decreased with increasing concentration between 25–75 mg/L ABA treatments, whereas concentration showed a consistent trend with fructose and glucose sugar content between 25–100 mg/L GA_3 treatments (Figure 1B and 1C). Glucose and fructose contents were maintained around 20 mg/g FW during development, and glucose sugar content of ABA sprayed at 90 days after flowering was at 21.3 mg/g FW, whereas the GA_3 treatment was at 26.2 mg/g FW, a difference of 5 mg/g FW (Figure 1C).

PsSUS4 and PsSPS2 genes in response to exogenous ABA and GA_3. *PsSUS4* and *PsSPS2* are sucrose synthase and sucrose-phosphate synthase genes, respectively, that convert fructose to uridine disphosphate glucose (UDPG) and thus synthesize sucrose during fruit development, and exogenous ABA and GA_3 exhibited the same pattern of changes in the *PsSUS4* and *PsSPS2* genes (Figure 2A and 2B). ABA treatment significantly increased the relative expression of *PsSUS4* and *PsSPS2* genes at 90–100 days after flowering, as shown by 75 mg/L > 50 mg/L > 25 mg/L > control; GA_3 regulated both genes significantly less than control at 90–110 days after flowering, and this negative regulation became more significant with increasing GA_3 concentration, specifically 100 mg/L > 50 mg/L > 25 mg/L > control.

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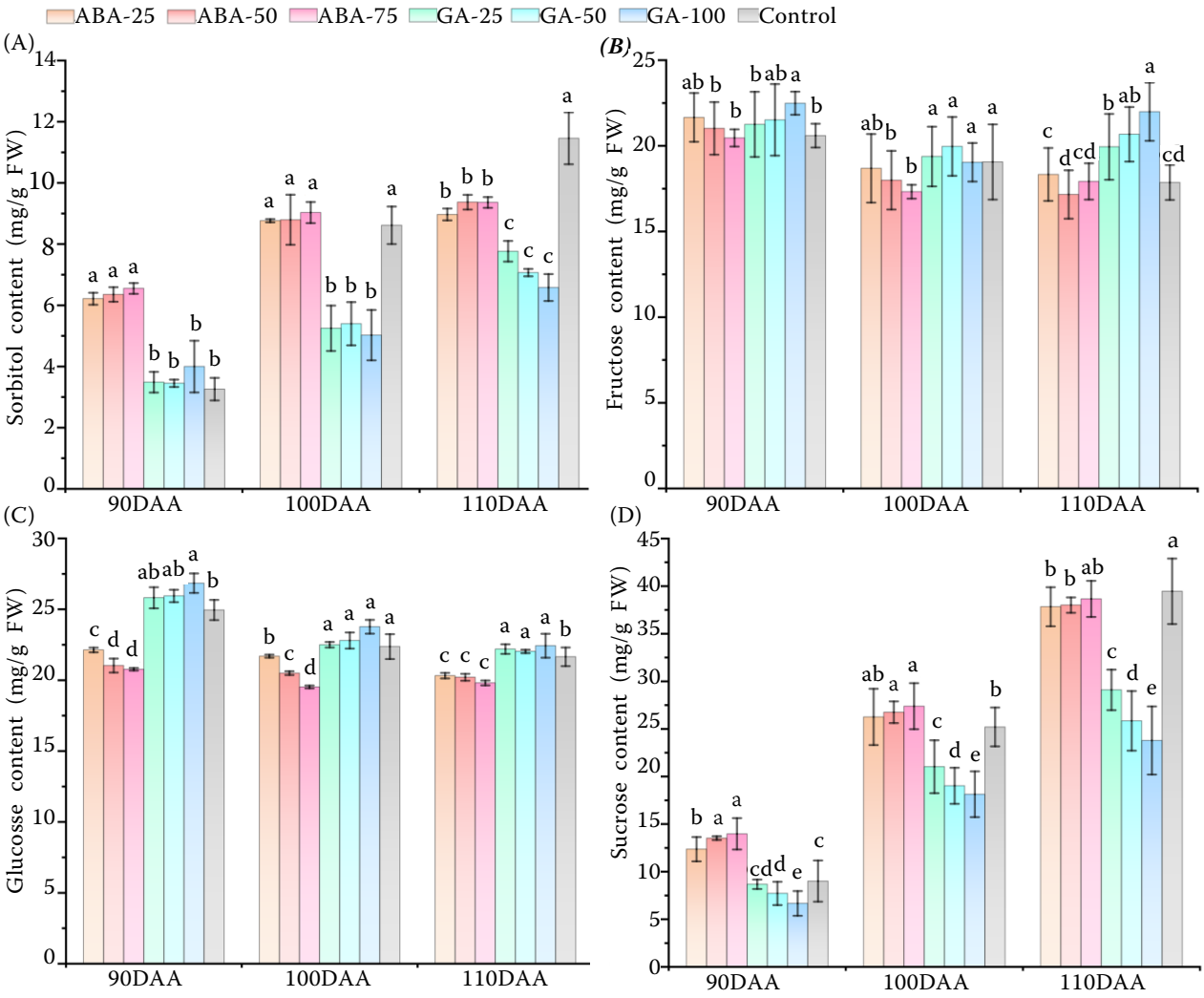

Figure 1. Effect of exogenous abscisic acid (ABA) and GA_3 on sugar fractions of 'Fengtang' plum; A – sorbitol; B – fructose; C – glucose; D – sucrose

*Error bars indicate the standard deviation between the three independent bioassays, [a–e]represent treatments showing significant differences at $P \leq 0.05$. 90DAA, 100DAA, and 110DAA indicate 90 days, 100 days, and 110 days after flowering, respectively

However, the *PsSUS4* and *PsSPS2* genes showed different trends in response to ABA and GA_3 at 90–110 days after flowering, with the *PsSUS4* gene increasing and then decreasing with fruit development, whereas *PsSPS2* showed a gradual decrease.

PsNINV gene response to exogenous ABA and GA_3. A total of three neutral convertase genes, *PsNINV1*, *PsNINV3* and *PsNINV4*, were screened in the previous study. Neutral convertases mainly convert sucrose transported extracellularly into the cytoplasm into fructose and glucose sugars during sugar accumulation. There were no significant differences in the *PsNINV1* and *PsNINV3* genes by ABA compared with control, and of interest was the increased expression of the *PsNINV4* gene at 100 days after flowering (Table 3). GA_3-treated fruits showed significantly higher gene expression compared to the control *PsNINV1*, *PsNINV3* and *PsNINV4* genes, with the highest gene expression in *PsNINV1* and a corresponding increase in *PsNINV1* gene expression with increasing concentration, and 100 mg/L GA_3 was significantly higher than control by a factor of 5.69, 5.26, and 3.46 over the three periods.Response of *PsSWEET4* and *PsSTP1* to exogenous ABA and GA_3. The sugar transporter protein genes *PsSWEET4* and *PsSTP1* behaved differently to ABA and GA_3 treatments (Figure 3). The gene expression of *PsSWEET4* and *PsSTP1* was significantly increased by ABA treatment com-

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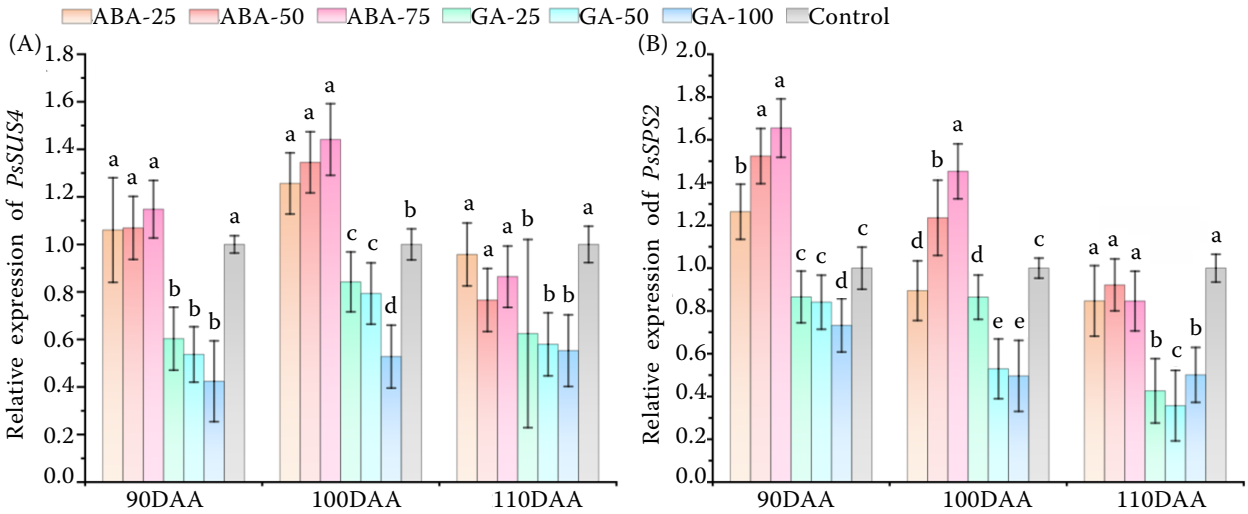

Figure 2. Regulation of *PsSUS4* and *PsSPS2* by exogenous abscisic acid (ABA) and GA_3

*Error bars indicate the standard deviation between the three independent bioassays, [a–e]represent treatments showing significant differences at $P \leq 0.05$. 90DAA, 100DAA, and 110DAA indicate 90 days, 100 days, and 110 days after flowering, respectively

Table 3. Regulation of *PsNINV1*, *PsNINV3* and *PsNINV4* by exogenous ABA and GA_3

Treatment	*PsNINV1* relative expression	*PsNINV3* relative expression	*PsNINV4* relative expression
90 days after flowering			
ABA-25	0.77 ± 0.13^{e}	0.98 ± 0.4^{c}	0.9 ± 0.15^{c}
ABA-50	0.69 ± 0.13^{e}	1.04 ± 0.4^{c}	0.93 ± 0.15^{c}
ABA-75	0.69 ± 0.4^{e}	1.14 ± 0.22^{c}	0.88 ± 0.13^{c}
GA-25	2.37 ± 0.35^{c}	1.54 ± 0.37^{a}	1.33 ± 0.12^{b}
GA-50	4.65 ± 0.4^{b}	1.34 ± 0.13^{b}	1.66 ± 0.13^{a}
GA-100	5.7 ± 0.13^{a}	1.37 ± 0.4^{b}	1.65 ± 0.15^{a}
Control	1.00 ± 0.07^{d}	1.00 ± 0.08^{c}	1.00 ± 0.07^{c}
100 days after flowering			
ABA-25	0.79 ± 0.13^{e}	0.96 ± 0.15^{d}	1.35 ± 0.13^{c}
ABA-50	0.95 ± 0.4^{d}	0.85 ± 0.17^{d}	1.27 ± 0.12^{c}
ABA-75	0.91 ± 0.12^{d}	0.97 ± 0.17^{d}	1.23 ± 0.17^{c}
GA-25	2.97 ± 0.4^{c}	1.86 ± 0.22^{b}	2.31 ± 0.13^{a}
GA-50	4.37 ± 0.17^{b}	1.57 ± 0.15^{c}	1.96 ± 0.13^{b}
GA-100	5.26 ± 0.16^{a}	2.35 ± 0.16^{a}	1.98 ± 0.17^{b}
Control	1.00 ± 0.08^{d}	1.00 ± 0.08^{d}	1.00 ± 0.06^{d}
110 days after flowering			
ABA-25	1.03 ± 0.16^{d}	1.03 ± 0.13^{c}	0.87 ± 0.17^{b}
ABA-50	1.37 ± 0.35^{c}	0.96 ± 0.37^{d}	0.8 ± 0.12^{c}
ABA-75	1.17 ± 0.13^{d}	0.87 ± 0.25^{d}	0.86 ± 0.13^{b}
GA-25	2.96 ± 0.16^{b}	2.33 ± 0.13^{a}	1.37 ± 0.13^{a}
GA-50	3.07 ± 0.37^{b}	1.96 ± 0.13^{b}	1.47 ± 0.12^{a}
GA-100	3.46 ± 0.12^{a}	2.51 ± 0.17^{a}	1.27 ± 0.17^{a}
Control	1.00 ± 0.03^{d}	1.00 ± 0.08^{c}	1.00 ± 0.08^{b}

*ABA-25, 50, 75 represents the concentration of exogenous abscisic acid (ABA) sprayed at 25 mg/L, 50 mg/L, and 75 mg/L. GA-25, 50, 100 represents the concentration of exogenous GA_3 sprayed at 25 mg/L, 50 mg/L, and 100 mg/L; control denotes clean water spraying; [a–d]indicate significant differences ($P \leq 0.05$) according to the Duncan test

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pared to control fruits at 90–100 days after flowering, and the expression of *PsSWEET4* was increased by 2.76 and 2.94 fold, respectively, by 75 mg/L ABA treatment, while the effect of 50 mg/L ABA treatment was slightly lower than that of 75 mg/L. At 110 days after flowering, *PsSWEET4* gene expression was significantly reduced in ABA-treated fruits, with expression in 75 mg/L ABA-treated fruits being only 63.2% of that in control fruits, and *PsSWEET4* was found to be significantly higher in fruits treated with 50–100 mg/L GA_3 than in control. Gene expression of *PsSTP1* was found to be significantly higher in 25 mg/L ABA and GA_3 than in control at 110 days after flowering, whereas gene expression of *PsSTP1* was significantly lower in 100 mg/L GA_3 treatment than in control.

Response of PsPGM1 and PsUGP to exogenous ABA and GA_3. Glucose is catalysed by Phosphoglucomutase (PGM) and UTP–glucose-1-phosphate uridylyl transferase (UGP) to form uridine diphosphate glucose (UDGP), which becomes an important substrate for the synthesis of sucrose. The trend of exogenous ABA and GA_3 on the expression of *PsPGM1* gene both showed a decrease and then an increase, but the expression of *PsPGM1* gene was not higher than that of CK in both treatments. It is noteworthy that the expression of ABA treatment was not significant with control at 90–110 days after flowering, whereas the expression of GA_3 treated fruits was significantly lower than that of control at 90–110 days after flowering in both treatments (Table 4). The expression patterns of exogenous ABA and GA_3 on *PsUGP1* and *PsUGP2* genes were different from those of *PsPGM1* gene, and the exogenous ABA-regulated *PsUGP2* gene showed a continuous decreasing trend with treatment time, changing from significantly higher than control at 90 days post-flowering to significantly lower than control at 110 days post-flowering, whereas the trend of the change of *PsUGP2* by GA_3 treatment was firstly upward and then downward, changing from significantly lower than control at 90 days post-flowering to significantly higher than control at 100 days to significantly lower than control at 110 days. The expression pattern of *PsUGP2* was different from that of *PsPGM1* gene.

PsHXK1/3 response to exogenous ABA and GA_3. The hexokinase gene (*PsHXK*) synthesizes glucose to G6P, which is then converted to UDGP by the *PsPGM1* and *PsUGP* genes, and ultimately synthesizes sucrose in the cytoplasm. The results showed (Figure 4) that 50 and 75 mg/L exogenous ABA treatments significantly promoted the expression of the *PsHXK1* gene at 90 days after flowering, while the expression of the *PsHXK1* gene in 25 mg/L exogenous ABA and 25–100 mg/L exogenous GA_3 treatments was significantly lower than that of the control treatment at 90–110 days after flowering, with the lowest expression being 0.2 times. Exogenous ABA treatment significantly promoted the expression of *PsHXK3* at 100 days after flowering, whereas exogenous GA_3 significantly suppressed the expression of the *PsHXK3* gene at 90 days after flowering, with the expression being only 0.5 fold of that of CK, and as the time of fruit development matured and the number of sprays increased, 50 mg/L exog-

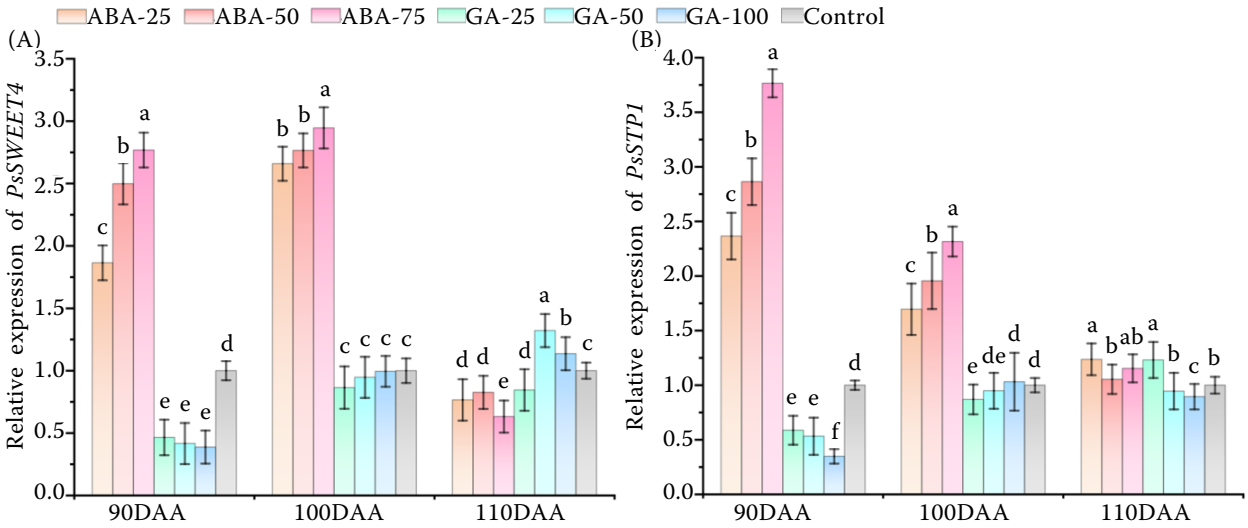

Figure 3. Regulation of *PsSWEET4* and *PsSTP1* by exogenous abscisic acid (ABA) and GA_3

*Error bars indicate the standard deviation between the three independent bioassays; [a–f]represent treatments showing significant differences at $P \leq 0.05$. 90DAA, 100DAA, and 110DAA indicate 90 days, 100 days, and 110 days after flowering, respectively

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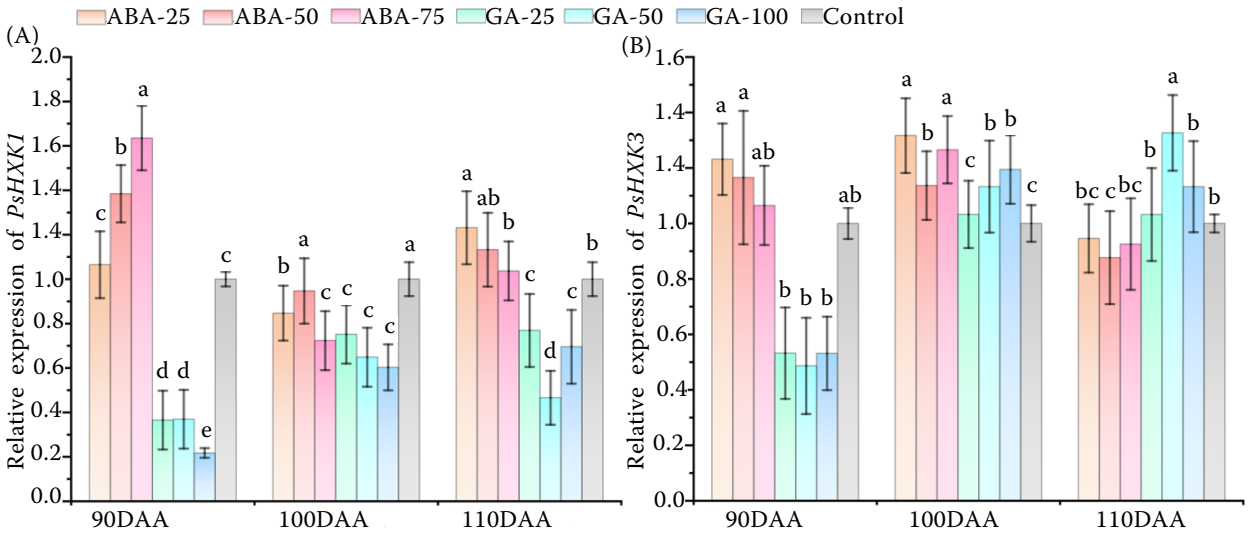

Figure 4. Regulation of *PsHXK1*, *PsHXK3* by exogenous abscisic acid (ABA) and GA_3

*Error bars indicate the standard deviation between the three independent bioassays, [a–f]represent treatments showing significant differences at $P \leq 0.05$. 90DAA, 100DAA, and 110DAA indicate 90 days, 100 days, and 110 days after flowering, respectively

enous GA_3 significantly promoted the expression of *PsHXK3* at 110 days after flowering.

Correlation analysis of key genes for sugar accumulation with sugar fractions and soluble solids. Correlation coefficient analyses of sugar fractions and soluble solids content with the expression of key genes in different treatments were done at 90 days, 100 days and 110 days after flowering by spraying different concentrations of exogenous ABA and GA_3. The results showed (Figure 5) that the trends of fructose and glucose sugars at 90–110days were indeed consistent, while the trends of sucrose, sorbitol and soluble solids were consistent. *PsNINV* gene expression had very high correlation coefficients with glucose and fructose content and very low correlation coefficients with sucrose and sorbitol as well as soluble solids; The genes *PsSUS4* and *PsSPS2* and *PsPGM1* were negatively correlated with fructose and glucose sugars and positively correlated with sucrose, sorbitol and soluble solids at 90–110 days after flowering; The *PsSWEET4* and *PsSTP1* genes were negatively correlated with fructose and glucose sugars and positively correlated with sucrose, sorbitol, and soluble solids at 90–100 days after flowering.

DISCUSSION

Exogenous ABA increases soluble solids content and delays hardness decline. As one of the five major phytohormones, ABA is widely distributed in tissues and organs of higher plants in response to external environmental signals (Yoshida et al. 2019; Gupta et al. 2022). Different concentrations of ABA treatments significantly increased the soluble solids and sugar content of apple (Sun et al. 2019), blueberry (Qu et al. 2017), and raspberry (Li et al. 2019), Kumar et al. (2019) spraying 2.84 mmol/L ABA not only resulted in early ripening of figs but also larger and less hard fruits than the control. In our study, we found that externally applied 25–75 mg/L ABA increased the soluble solids of ripening fruits of 'Fengtang' plum, and this effect was cumulative with the number of sprays and with the maturity of fruit development, delaying the decline in fruit firmness, and the same results were obtained in apricot (Jia et al. 2022). This may be related to the promotion of the expression of the ABA receptor protein gene (PYL9) inhibiting the activity of downstream genes (Kai et al. 2019) and that spraying exogenous sucrose can co-modulate fruit quality with ABA (Luo et al. 2020; Xiong et al. 2020). Our results showed that 75 mg/L ABA was significantly lower than control after three times of spraying, while only 25 mg/L ABA significantly promoted the increase of single fruit weight, which may be related to the concentration of spraying and the number of times of spraying, low concentration sprayed many times and high concentration sprayed few times to improve the effect of single fruit weight, too high concentration sprayed many times instead of inhibiting the fruit development. It was found

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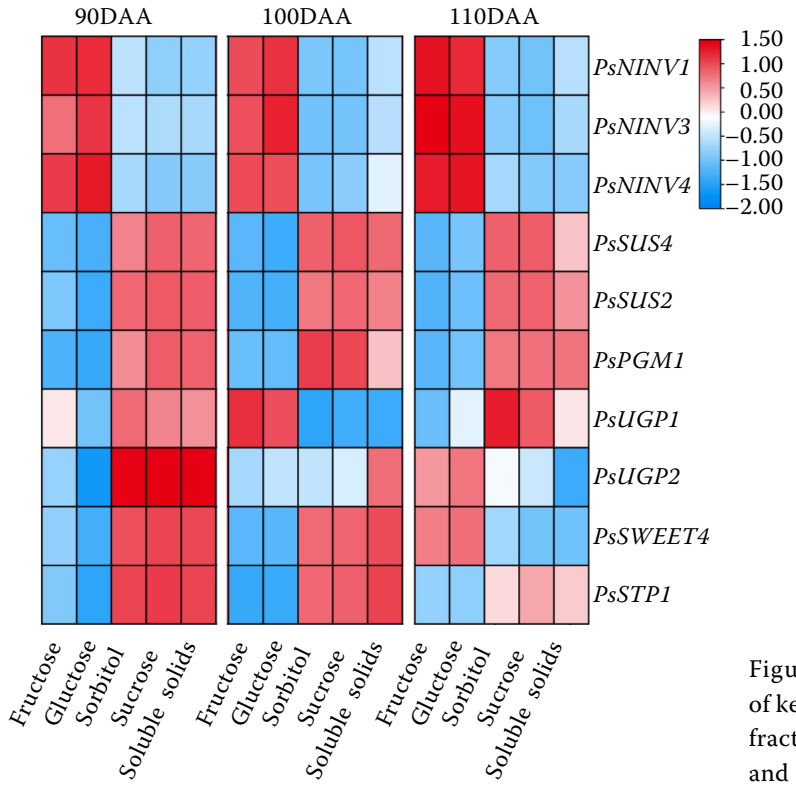

Figure 5. Heat map of correlation analysis of key genes for sugar accumulation with sugar fractions and soluble solids at 90 days, 100 days and 110 days after flowering

that high concentrations of ABA did not significantly regulate single fruit weight in grapes (Li et al. 2021), strawberries (Luo et al. 2019) and sweet cherries (Time et al. 2021), but increased soluble solids accumulation, which is in keeping with our conjecture.

Exogenous ABA promotes sucrose and sorbitol accumulation and reduces glucose and fructose content. Sucrose, glucose, fructose and sorbitol are the main sugar fractions in all drupe fruits (Baldicchi et al. 2015; Desnoues et al. 2018), Wang et al. (2023) determined the content of sugar fractions in different plum varieties and found that sucrose differed significantly among the varieties; the 'Amber Jewel' variety had the highest fructose content and the lowest sucrose content (Singh et al. 2009). Soluble sugars in apples and pears are dominated by fructose accounting for 40–60% of total soluble sugars, followed by sucrose (Ackermann et al. 1992; Zhang et al. 2014), whereas glucose and fructose content declined prior to the ripening of the fruits of the 'Xiyang' plum (García-Mariño 2008), 'Furong' plum were characterized by a glucose content increased and sucrose and fructose content decreased (Jiang et al. 2018). In this study, sorbitol and sucrose contents were significantly increased and glucose and fructose contents were decreased at 90 days after exogenous ABA treatment, which is consistent with the performance of fructose and glucose during ripening in apricot (Gou et al. 2023), but this advantage disappeared at 100 and 110 days after flowering, which may be mainly due to the increase in the number of times of spraying and the increase in the concentration of exogenous ABA, which also produces a large amount of endogenous ABA to promote ripening during the ripening of the fruits. The increase in exogenous ABA may lead to a negative regulatory effect, as the fruit itself produces a large amount of endogenous ABA to promote ripening during ripening.

Reduction of soluble sugar content and delay of fruit ripening by exogenous GA_3. Our study was conducted in the hope that exogenous GA_3 treatment would thereby regulate the sugar content of 'Fengtang' plum fruits, The results showed that sucrose and sorbitol contents were significantly lower than control at the same time point by spraying exogenous GA_3, and soluble solids content was reduced, The possible reason analysed was that GA_3 converted sucrose and sorbitol into glucose and fructose via the *PsNINV* gene, which physiologically delayed fruit ripening, and exogenous GA_3 on persimmon also delayed fruit ripening. However, in the study of 'Cuiguan' pear by Li et al. (2015), it was found that GA_3 treatment could increase the sugar content

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Table 4. Regulation of *PsPGM1*, *PsUGP1* and *PsUGP2* by exogenous ABA and GA_3

Treatment	*PsPGM1* relative expression	*PsUGP1* relative expression	*PsUGP2* relative expression
90 days after flowering			
ABA-25	1.03 ± 0.17^{a}	1.23 ± 0.17^{a}	1.53 ± 0.12^{a}
ABA-50	0.99 ± 0.13^{a}	1.03 ± 0.16^{b}	1.63 ± 0.13^{a}
ABA-75	0.95 ± 0.15^{a}	0.96 ± 0.13^{c}	1.56 ± 0.13^{a}
GA-25	0.65 ± 0.24^{b}	0.89 ± 0.13^{c}	0.65 ± 0.17^{c}
GA-50	0.6 ± 0.25^{b}	0.93 ± 0.14^{c}	0.69 ± 0.13^{c}
GA-100	0.44 ± 0.29^{b}	0.97 ± 0.14^{c}	0.76 ± 0.13^{c}
Control	1.00 ± 0.05^{a}	1.00 ± 0.08^{b}	1.00 ± 0.06^{b}
100 days after flowering			
ABA-25	0.87 ± 0.16^{a}	0.85 ± 0.13^{c}	1.24 ± 0.12^{a}
ABA-50	0.79 ± 0.15^{a}	0.9 ± 0.13^{c}	1.37 ± 0.29^{a}
ABA-75	0.83 ± 0.4^{a}	0.81 ± 0.15^{c}	1.43 ± 0.13^{a}
GA-25	0.43 ± 0.15^{b}	1.16 ± 0.13^{a}	1.32 ± 0.17^{a}
GA-50	0.4 ± 0.17^{b}	1.04 ± 0.12^{b}	1.3 ± 0.4^{a}
GA-100	0.39 ± 0.13^{b}	0.98 ± 0.17^{bc}	1.4 ± 0.37^{a}
Control	1.00 ± 0.08^{a}	1.00 ± 0.03^{b}	1.00 ± 0.06^{b}
110 days after flowering			
ABA-25	0.9 ± 0.17^{b}	0.63 ± 0.16^{b}	1.05 ± 0.13^{a}
ABA-50	0.98 ± 0.24^{a}	0.62 ± 0.06^{b}	0.29 ± 0.16^{c}
ABA-75	1.03 ± 0.13^{ab}	0.53 ± 0.11^{c}	0.58 ± 0.15^{b}
GA-25	0.91 ± 0.13^{b}	0.58 ± 0.12^{b}	0.91 ± 0.13^{a}
GA-50	0.73 ± 0.12^{c}	0.35 ± 0.05^{d}	0.84 ± 0.24^{a}
GA-100	0.9 ± 0.14^{b}	0.52 ± 0.12^{c}	0.84 ± 0.13^{a}
Control	1.00 ± 0.06^{a}	1.00 ± 0.05^{a}	1.00 ± 0.08^{a}

*ABA-25, 50, 75 represents the concentration of exogenous ABA sprayed at 25 mg/L, 50 mg/L, and 75 mg/L; GA-25, 50, 100 represents the concentration of exogenousGA_3 sprayed at 25 mg/L, 50 mg/L, and 100 mg/L; control denotes clean water spraying; $^{a-d}$indicate significant differences ($P \leq 0.05$) according to the Duncan test

in the fruit during the fruit expansion stage by increasing the gene expression of *PbSPS*, *PbINV* while decreasing the expression of *PbSUS* genes and thus increasing the sugar content in the fruits, which may be due to the differential performance due to the different species.

Regulation of key genes for sugar accumulation by exogenous ABA and GA_3. At the molecular level, ABA treatment significantly increased the expression of *PsSWEET4* and *PsSTP1* at 90—100 days after flowering, as well as the gene expression of *PsSUS4* and *PsSPS2*, but the overall gene expression at fruit ripening was not significantly different from that of the control, and such a result corresponded exactly to the accumulation and content of fruit sugars. It was shown that in 'Huangguan' plum the sugar transporter protein genes *PsSWEET2a-like* and *PsSWEET17-like* were significantly positively correlated with fructose and glucose accumulation, and significantly negatively correlated with sucrose accumulation (Yu et al. 2021). Whereas in apple, the *MdSWEET17* gene is negatively correlated with fructose synthesis (Yang et al. 2018), and sugar accumulation at maturity is mainly related to the transmembrane transport of sugar fractions (Kobashi et al. 2001), in 'Fengtang' plum, *PsSWEET4* and *PsSTP1* just happen to play transmembrane transport play a key role.

CONCLUSION

Exogenous ABA catalyses the conversion of glucose and fructose to sucrose by increasing the expression of the fruit sugar transporter-related genes *PsSWEET4* and *PsSTP1* and the sucrose synthase genes

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PsSUS4 and *PsSPS2* at 90–100 days after flowering and promotes fruit maturation; exogenous GA_3 delays fruit ripening by promoting the catabolism of cytoplasmic sucrose into fructose and glucose by the activity of the neutral convertase gene *PsNINV1/3/4*. In production, the present results can guide fruit production to increase sugar content before harvesting, and to extend the fruit harvesting period thus avoiding concentrated fruit ripening. In terms of research, how *PsSWEET* acts as a sugar transporter gene between source-repository; *PsSUS* as a functional gene, the exploration of transcription factors upstream of *PsSUS*, the present results can provide a basis for more in-depth mechanistic studies.

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